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MORPHOGENETIC METHOD
IN COMMON BUCKWHEAT BREEDING
(*Fagopyrum esculentum* Moench)

Monography

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COCNCLUSION

In order to understand biological phenomena at the systemic level, it should be taken into consideration that biological processes in cells, organs and organisms are driven not only by molecular and genetic regulation. The necessary attributes of biological processes are the transportation of molecules and movement of material masses, which occur in spatial domains with different geometry. Among the biologically significant results of these processes is the change in geometry of these domains, i.e., morphodynamic processes which are observed during the biological systems movement and growth, and should be regarded as mechanical phenomena. The shape of an entire organism and its anatomical structures is both a result and a diagnostic sign of organism functioning – from genes expression up to transportation processes (Nikolaev, 2013).

Metamerism (body structure composed of the repeating elements) is common for all higher plants. The anlage and development of each metamer requires certain amount of time (morphochron), therefore their quantity inevitably transforms into quality: dimensions of an annual life form are strictly limited by the warm season boundaries set by the local climate. Of course, no single plant represents a mechanical pile of metamers, and each phytomer shows its own peculiarities, it being especially visible in the evolutionary advanced taxa. However, the quantitative account of phytomers may be sufficiently informative in this case, too.

Buckwheat is a plant with a comparatively simple morphological organization, therefore, it can be used as a convenient model object for studying metameric regularities. It has been clearly demonstrated in numerous breeding and genetic experiments, in which metamerism served as the background for selecting populations and describing their structure. The All-Russian Research Institute of Legumes and Groat Crops in Orel has developed a school of efficient buckwheat breeding that is widely practicing the phytomer-based approach in describing plant architecture. This approach has formed empirically when solving the problems of breeding for earliness, as well as when describing a series of morphological mutations. The approach differs from the one accepted in botany and ideologically is closer to the modular approach (see Harper, 1977).

Besides, it proved to be highly informative and efficient when analyzing changes in buckwheat biology during the expansion of the crop distribution area practically up to the northern limits of agriculture.

It has been established that common buckwheat retains the main specific features such as the intensive unlimited growth type, allogamy, heterostyly, remontancy, weak homeostasis in fruit development, and has insignificantly decreased heat and water demand (Fesenko N.V., 1983; Lakhanov et al., 2004). The advance of buckwheat from the center of its origin (subtropics of Southern China) to the areas with moderate climate was followed by the vegetative period shortening, which was due to transformation (reduction) of

the branching system. Since the development of generative organs has changed to a lesser degree, the decrease in number of vegetative nodes per main stem and first-order branches has led to a significant increase in the ratio between generative and vegetative metamers, and, as a consequence, to a sharp increase in the dynamics of flowering of both individual inflorescences and of the entire plant. As a result, a tendency towards a partial separation between the vegetative growth and the fruit formation phases has started to show.

The given simplified ('working') outline of regularities of buckwheat adaptation to the northern climate (in a wide sense) is based on a direct comparison of local (early-ripening) and exotic (late-ripening) accessions in the field. An earlier, similar comparison gave a reason to Soviet botanists to separate the East-European buckwheat into a 'common' subspecies (including 'almost photoneutral' cultivars capable of yielding seed under long day), while the highly photoperiod-sensitive cultivars from the global buckwheat collection were attributed to the 'multifoliate' subspecies (subsp. *multifolium* Stol.) that featured the delayed breaking into blossoming and vigorous biomass development. Such a classification is also quite acceptable as a 'working' one and convenient for the East-European breeders. The 'multifoliate' subspecies embraced all cultivars from Eastern Asia where the northern boundary of agriculture lies much more to the south than in Europe.

At the same time, a local 'working' classification that distinguishes cultivars of 'summer' and 'autumn' type has been developed in Eastern Asia. The information from local authors and personal observations make it possible to conclude that, in fact, there exists a common, productive buckwheat morphotype that formed at the time and place of buckwheat domestication: today there exists there a set of cultivars with a broad ripening range – from ultra-early (60 days) up to late ones (90 days). However, all these cultivars have high photoperiod sensitivity, and when they get into the longer day conditions in Northern China, Korea and Japan, they delay the beginning of flowering and produce excessive biomass at the expense of seed yield. This is the behavior of the 'autumn' type cultivars that change their morphotype into an earlier-ripening one with a higher 'grain content' when sown in August (under short day). These are the regions where strong typhoons happen regularly and where buckwheat has been used as a backup crop that is planted to compensate for the destroyed rice crop. A less sensitive 'summer' buckwheat type (cultivars suitable for spring sowing) has formed here in later times as a result of folk breeding. Most likely, these were the cultivars of this particular type that were used for expanding the distribution of the crop in the northwestern direction (which is evidenced by a lower photoperiod sensitivity in most populations in the countries of Europe and the former USSR).

The widest variation in duration of the buckwheat vegetative period that served as a basis for the significant expansion of the distribution area (while high requirements to heat and moisture persisted) and for the unlimited

growth type is ensured due to the wide genetic variability of the main trait that characterizes plant architecture, that is, of the number of vegetative metamers (nodes) per plant shoot of any order.

Our research has demonstrated not only the adaptive nature of changes in plants' vegetative organs, but also the adaptive significance of polymorphism of this character. In general, adaptation is interpreted as an entire system of reactions aimed at maintaining dynamic equilibrium between the organism and the environment (Shmalgauzen, 1968; Altukhov, 2003), ensured by the adaptive genome structure (Zhuchenko, 2005) and 'channeled' by the life strategy of a species (Mirkin et al., 1999). The adaptive strategy places buckwheat among the aggressive competitor plants (Fesenko N.V. et al., 2006). Plants of this kind are typical of the ecologically favorable habitats and lack special adaptations to stresses of ecological nature. The main protective adaptations of buckwheat are the high vigor and competitive ability (long intensive growth) and the developed remontancy (prolonged flowering and fruit formation). Manifestation of these features is ensured by a high degree of heterosis in a population associated with the obligate cross-pollination of heterostyled components (Palilov, 1976) and the prevalence of growth processes in source-sink relations (Fesenko N.V. et al., 2006).

Adaptive reactions are weak in individual buckwheat plants, therefore a significant role in this respect is played by the population. The characteristic features of buckwheat populations are the clearly expressed structure of reproduction mechanisms (heterostyled system) and of the rhythm of ontogenesis (stem branching zone (SBZ) system) in plants. Their functioning is ensured by genetic mechanisms responsible for the maintenance of homeostasis within a population and its reproduction in progenies (Palilov, 1976; Fesenko N. N., Gurinovich, 1999; Fesenko N. N., Fesenko I. N., 2005; Fesenko N. V. et al., 2006).

A peculiar feature of the SBZ system is the presence in all populations of a group of morphotypes with different rhythms of development and adaptive role. The modal SBZ morphotypes that quantitatively prevail in a population characterize the adaptive norm of the population, that is, the degree of its adaptation to the growing season duration in the habitat. These morphotypes represent the adaptive nucleus of a population. At the same time, a population certainly contains an insignificant group of SBZ morphotypes which occupy extreme positions in the total SBZ range. They have an insurance function to be performed in cases of abrupt environmental change when these morphotypes acquire the role of 'adaptive nucleus' in new conditions and ensure the high rhythm of adaptive transformations in buckwheat. The extended flowering period ensures cross-pollination of morphotypes that differ by the developmental rhythm and thus preserve heterogeneity of the population. The range of variation in populations originating from the sufficiently 'comfortable' regions of the East European part of buckwheat distribution area may be quite wide and span

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from early to ultra-late SBZ morphotypes, which are characteristic of populations from subtropical regions. Therefore, the species *Fagopyrum esculentum* Moench may be regarded as a continuous row of SBZ morphotypes with different developmental rhythms.

The adaptive process in a population leads to the formation of a ratio between SBZ morphotypes that differ by their developmental rhythm and vigor. This broadens the adaptive norm of a population, and thus it acquires the status of the intraspecific adaptation unit.

The morphological system of buckwheat adaptation functions in the following way: due to the fluctuation of the weather factors, the periods favorable for fruit formation coincide with the development rhythm of a plant belonging to this or that SBZ morphotype. It determines the advantage of this morphotype in terms of its contribution to the yield of the population. In the long run, the random variation of weather factors approaches the mean annual rhythm of climatic conditions in a locality, which allows a well-established population to accumulate the SBZ morphotypes that are most productive under these particular conditions. Thus, the life of a population becomes subjected to natural selection aimed at increasing its adaptability to regional conditions.

An example of natural selection is the breeding of the first released buckwheat cultivar Bogatyr', when a local low-productive and early ripening population has been transformed over a number of years into a highly productive mid-season cultivar. This result could be achieved through the selection of the optimal (more early) sowing time on rich soils (Fesenko N.V., 1983). This combination provided adaptive advantages for more late (hence, more productive) morphotypes and led to their accumulation in the population and an increase in crop yield. For several decades, said cultivar has been holding leading positions in the USSR in terms of the occupied growing areas.

The involvement in our breeding experiments of an interspecific hybrid (*F.esculentum* x ultra-late wild species *F. homotropicum*) may serve as an example of buckwheat adaptation to a shorter growing season. The hybrid was a too late-ripening one for conditions of the Orel Province, however, after three cycles of field cultivation (without improvement through selection, but with harvesting on the dates accepted for the mid-season cultivars) duration of the vegetative period of the interspecific hybrid population has dropped down to the level that was close to that of mid-season indeterminate cultivars. At the same time, the average number of vegetative nodes per stem in the adapting population has reduced from 6.7 to 5.5, and the number of vegetative nodes per plant dropped from 22.7 to 17.4.

The ability of buckwheat to adaptively change the population structure should be taken into consideration in seed production. Especially it relates to early cultivars, because systematic delays in harvesting may lead to an extension of the vegetative period of a population and to the loss of earliness.

As the local populations were approaching the latitude close to the northern boundary of agriculture, the adaptive potential of the SBZ system kept

depleting, and the branching system got involved in the adaptive process by means of inclusion in the adaptive genome of *lsb*, a mutant allele with a positive evolutionary status, which determines the reduction of the vegetative branching zone (the synchronized onset of flowering of shoots in plants with limited branching ensures dynamism of the process and shortens flowering duration). This made formation of more early-ripening morphotypes possible and facilitated the expansion of the buckwheat distribution area, which allows one to regard this phenomenon as an act of adaptiogenesis.

According to the analysis of the obtained material, the leading mechanism of changing the protective and adaptive complex in *Fagopyrum esculentum* is morphogenesis with reduction of the main adaptive properties of the species (growth processes intensity and remontancy) as its main vector.

In general, evolution of buckwheat under cultivation followed the regularity established by N.A. Maisurian for annual dicotyledons: a characteristic tendency in plants domestication is the reduction of branching (Maisurian, 1960). During the last 50 years, this vector of buckwheat evolution under cultivation has been sufficiently corrected by the breeders' efforts.

The further progress in buckwheat breeding for higher yields within the optimal growing season was associated with raising the branching potential due to the improvement of plants' metameric architecture. For the indeterminate cultivars Yesen', Ballada and Molva it was achieved through combining partial reduction of the vegetative organs in upper branches with increasing the number of vegetative nodes per stem and entire plant.

Breeding of determinate cultivars was accompanied by an even more noticeable increase in the branching potential (1.4–1.5 times higher than in cv. Bogatyr'). It is determined by genetic control of the generative organs growth in a plant, which results in a comparatively shorter stem, increased lodging resistance and tolerance to dense planting, thus strengthening the role of lower-layer branches in the production process. A decrease in the number of generative nodes per shoot makes flowering and ripening more uniform and, as a consequence, maintains the optimal duration of the vegetative period in the morphologically more late-ripening determinate cultivars. Mutation of the determinate type of growth does not influence roots development (Kolomeychenko, Savkin, Fesenko A.N., 1999), therefore it may be supposed that an increase in yields of the determinate cultivars is partially linked with formation of a root system that is adequate to the increased branching potential.

Thus, there is a direct link between the higher yields of mutant buckwheat cultivars of the new generation and the changes that occurred in plant architecture and raised the branching potential in these cultivars along with the maintenance of the vegetative period duration that is optimal for the mid-season cultivars. The correlation analysis has revealed a significant relation between the yielding ability and such features of plant architecture as the number of vegetative nodes per stem and plant, as well as the contribution of individual

branches to the general branching potential of buckwheat plants of different morphotype.

As a result of the performed research, buckwheat is used as an example for suggesting an integral indicator that characterizes a plant as a holistic functional and dynamic system capable of self-development and self-replication. This indicator is the metameric architecture of a plant (cultivar) which characterizes the rhythm of formation, number, size and spatial location of plant metamers, as well as duration of the vegetative period and potential productivity of a plant (cultivar). The use of this indicator provides prerequisites for a shift in breeding technologies from the 'probabilistic' method to a systematic 'construction' of morphotypes with high productivity characteristics. The key indicator that characterizes adaptive and production capabilities of buckwheat cultivars is the average number of vegetative nodes per plant (the branching potential) of a cultivar. The number of vegetative nodes per stem determines the time of plant transition to flowering (i.e., the vegetative period duration); the number of vegetative nodes in the first order branches determines duration of flowering and fruit formation (i.e., generative period duration). The metamers that most completely characterize productive properties of buckwheat plants are the vegetative and generative nodes which serve as indicators of the source-sink systems development. Their number determines potential productivity of a plant (biomass), while their ratio determines the degree of assimilate translocation to seeds (the harvest index, HI), that is, characterizes source-sink relations in the accessions involved in breeding process.

The use of plant architecture in breeding has a number of advantages. Buckwheat is a cross-pollinated crop, therefore a selection using the resulting indicators (e.g., biomass, seed productivity, plant HI, inflorescence size and 'grain content', etc.) is possible only after the plants' cross-pollination, which decreases efficiency of such selection. Determination of plant architecture indicators is possible before or at the beginning of flowering, which makes the purposeful outcrossing of the required genotypes possible.

Besides, the previous breeding experience shows a limited use in breeding of the traits characterizing plant vigor (plant biomass, seed mass per plant, inflorescence size, etc.), as breeding aimed at improving these traits may lead in a crop stand to a decreased seed yield, though an individual plant analysis always finds a positive correlation between vigor and seed productivity. It is most apparent in buckwheat breeding. Selection towards the resulting characters proved to have low effectiveness not only because buckwheat is a cross-pollinated crop and it is impossible to fix fortunate gene combinations promoting high productivity in this crop. This selection was found to have a stabilizing effect which does not let buckwheat as a species to overcome its drawbacks when grown on rich soil (strengthening of competition under worse illumination, tendency to excessive growth, lodging, etc.) An increase in buckwheat yielding capacity requires reconstruction of its protective and adaptive complex (Fesenko N.V. et al., 2006).

According to our research, the progress in breeding is achieved due to the use of mutations which reduce potential productivity of buckwheat plants. For instance, the plants with limited branching were characterized by low seed productivity under wide row planting, however due to a higher tolerance to dense planting they exceeded in this regard the normally branching ones planted in rows.

The improvement of the determinate cultivars architecture is of the highest interest for breeding purposes. The determinate cultivars have a reduced reproductive part of the shoot and sharply strengthened vegetative organs, however, there is no decrease in the assimilate translocation to seeds. Such forms with the changed physiological correlations in development are of special importance, as progress in breeding is often connected with overcoming the established correlations.

Obviously, improvement of the balance in source-sink relations in the vegetative and reproductive organs in a determinate form is achieved not through the increase in total metamers, but through optimization of plant system morphogenesis, i.e., synchronization of flowering within a shoot ensures assimilate import into the ovaries. At the same time, seeds mature on the background of their roots and leaves high providing, which ensures an increased drought resistance in determinate cultivars (Fesenko A. N., Martynenko, Selikhov, 2012).

A reduced number of inflorescences in shoots of modern determinate cultivars is partially compensated by the number of flowers per inflorescence. Despite a somewhat lower number of flowers per plant, the assimilate translocation to the forming seeds in them is even stronger in comparison with the indeterminate cultivars (Fesenko A.N. et al., 2014).

Among positive features of these determinate cultivars are a higher drought resistance, a better response to fertilization, uniform ripening, resistance to lodging during ripening, and suitability for combine harvesting. These features have determined the wide distribution of these cultivars, which occupy over a half of all the areas under buckwheat in Russia (Fesenko A. N., Martynenko, Selikhov, 2012). Thus, it is necessary to study possibilities of improving plant architecture in determinate cultivars.

The global practice shows that high commercial yielding ability is typically displayed by the crops capable of forming a dense, well illuminated agrocenosis in which harmonious development of plants is maintained. A prerequisite for that is the limitation of competitive responses of plants.

The problems of increasing the plant habitus efficiency and shortening the extensive period of flowering and fruit formation are the factors of increasing yielding ability. According to our research, at present it can be achieved through reducing the secondary branching.

Regulation of the number of vegetative nodes in branches (transformation of the vegetative organs' architecture) may be done by using two mutations. The first one is the blocked branching mutation which causes a complete or partial suppression of the axillary meristems development. This mutation has been little studied, so far, however our research shows that its use may be promising for suppressing the development of the lower branches which make practically no contribution to seed productivity of plants belonging to cultivars of different morphotype planted in rows. It is demonstrated that the use of this mutation promotes tolerance to dense planting of indeterminate plants. The use of this mutation in breeding determinate cultivars requires further investigation.

The second mutation is the well-studied limited branching mutation (*lsb* allele). The *lsb* allele-influenced decrease in the vegetative nodes number in upper branches is accompanied by an increase in flowering vigor, earliness and HI, but the branching potential and plant productivity get reduced. At the same time, the productivity potential of plants with limited branching is realized in denser stands better than that of the normally branching plants, i.e., a higher tolerance to dense planting is displayed. The latter is characteristic of both indeterminate and determinate plants with limited branching.

According to our opinion, at present, the combination of the 'limited branching' and 'determinate growth type of a shoot' are the main parameters of the ideotypes of cultivars being created for regions of this country which differ by temperature and moisture availability. The use of this combination makes it possible to increase the branching potential and yielding ability of new buckwheat cultivars along with maintaining the optimal duration of the vegetative period. There exists a reliable correlation between such characters as the 'number of nodes in SBZ' and the 'vegetative period duration', as well as between the 'number of vegetative nodes in branches' and the 'generative period duration'. No correlation was found to exist between the 'number of nodes in SBZ' and the 'limited branching'. It makes it possible to vary duration of the interphase periods for the sake of breeding purposes by means of changing plant architecture.

At present, the breeding of high yielding determinate cultivars is carried out by combining in a population the high flowering and fruiting vigor with an increased branching potential by means of selecting morphotypes with a bigger number of nodes in SBZ, and by partially reducing the branching zone in the upper branches.

The combined action of *lsb* and *d* mutant alleles weakens the vegetative growth and raises HI, thus increasing plants' tolerance to crop overcrowding. In this case, a higher productivity in a cenosis is noted for the intermediate morphotypes (with a partial reduction of vegetative organs in the upper branches).

The optimal ratio between morphotypes with different degrees of branching reduction in a population is still to be specified.

The improvement of plant architecture by using *lsb* and *d* mutant alleles made it possible to combine the high branching potential of the determinate morphotype with high fruiting vigor and uniform ripening of the morphotypes with limited branching in order to create a mid-season, high yielding cultivar. This approach has been used to develop such mid-season cultivars as Devyatka (commercialized in Regions: Central, Central Black Soil, North Caucasus, Urals and Far East) and Dialog (commercialized in Regions: Central, Volga-Vyatka, Central Black Soil, Middle Volga, Urals and West Siberian). Both cultivars are characterized by an increased number of nodes in SBZ, as well as by a bigger share of plants with limited branching in comparison with the standard cv. Dikul' (Fesenko A.N., Martynenko, Fesenko N.V., Mazalov, 2012).

Obviously, the physiological mechanism that promotes tolerance to crop overcrowding in determinate plants with limited branching is based on a higher efficiency of the photosynthesizing apparatus in reducing competition for light, which increased assimilate translocation to seeds along with a comparative strengthening of the generative organs (i.e., an increased generative load on the vegetative node). Regulation of the generative load on the vegetative node in determinate cultivars is possible not only by means of reducing the secondary branching, but also by carrying out selection for a bigger number of inflorescences per shoot.

It has been established that the number of inflorescences per shoot of determinate buckwheat cultivars can be increased through breeding. This phenomenon is of scientific and practical interest as an example of natural micro-evolutionary processes occurring in buckwheat. Morphotypes with a larger number of inflorescences are characterized by a higher general productivity and seed productivity, HI and tolerance to dense planting. Strengthening of the reproductive zone of shoots is considered as a promising technique in breeding high yielding determinate cultivars.

The ways outlined in the present work and aimed at improving buckwheat plants architecture in no way reject the use of traditional methods of selection on the basis of plant productivity, 'grain content' of inflorescences, etc. Nevertheless, the change of architecture is the key factor in successful restructuring of the protective and adaptive complex in buckwheat. Further research in this direction should play the major role in increasing yields of this crop.